IDENTIFICATION OF THE SOCIAL AND COGNITIVE PROCESSES UNDERLYING HUMAN CUMULATIVE CULTURE

Dean, L.G., Kendal, R.L., Schapiro, S.J., Thierry, B. & Laland, K. N.

SUPPLEMENTARY ONLINE MATERIAL

This document contains additional methodological details and results to those given in the main article.

METHODS

We exposed social groups of 3-4 year-old children, adult and juvenile chimpanzees and capuchin monkeys to an experimental puzzle box (Figure 1, Figure S1) that could be solved at three sequential levels to retrieve rewards of increasing desirability. The study was designed to evaluate eight separate hypotheses concerning the factors necessary for cumulative cultural learning (Table S5, below). Two experiments were conducted. The first involved presenting groups of naive subjects with the puzzlebox, across two conditions (an 'open' condition where groups could gain access to all stages, and a 'scaffolded' condition, where guards prevented access to the manipulandi associated with higher stages until performance at the lower stage reached criterion), and recording which individuals interacted with it, when and how as well as who observed these interactions. This experiment was carried out with all three species, although the capuchins experienced only the scaffolded

condition. The second experiment was carried out with chimpanzees only and involved training demonstrator animals, of high and low status, to solve the box and retrieve food effectively. These trained individuals were then reintroduced into their native groups with the puzzlebox, and allowed to demonstrate successful solutions. We again monitored which individuals interacted with the puzzlebox as well as when, how and who observed these interactions. This second experiment was designed to determine whether the failure of the chimpanzees to achieve high-level solutions in the first experiment could be attributed to an absence of quality demonstration, as well as to evaluate whether the status of the demonstrator affected the likelihood of individuals adopting a behaviour pattern.

Subjects

(i) Chimpanzees. Subjects were housed at the Michale E. Keeling Center, MD Anderson Cancer Center, Bastrop, TX, USA. They were tested in the outdoor portion of their enclosures, which are octagonal corrals 24.3 metres in diameter. Chimpanzees were not food deprived before the experiment, but were not tested within an hour of a large feed.

Table S1. Chimpanzee groups participating in the experiment.

Experiment	Group Number	Condition (Exp 1)/ Demonstrator rank (exp 2)	Number of males	Number of females	Number of adults	Number of sub-adults/ juveniles	Mean age of group (yrs) (± standard error)
1	C1	Open	4	4	7	1	25 (±2.60)
1	C5	Open	4	6	8	2	19.3 (±2.03)
1	C6	Scaffolded	3	5	8	0	32.4 (±3.59)
1	C8	Scaffolded	2	5	6	1	31.6 (±6.17)

2	C2	High	7	6	12	1	26.5 (±3.39)
2	C3	Low	4	5	9	0	22.7 (±1.87)
2	C4	Low	2	9	10	1	23.5 (±3.40)
2	C7	High	2	6	8	0	31.6 (±3.39)

The 74 subjects were aged between 6 and 48 years old and were housed in 8 multi-male, multi-female groups, ranging in size from 7 to 13 individuals (Table S1).

(ii) Capuchins. Subjects were housed at the Centre de Primatologie, Strasbourg, France. The single population was tested in the outdoor portion of their enclosure, consisting of two interconnected runs measuring 45m^2 in total. The puzzlebox was placed at the end of the larger run with access allowed to both outdoor runs during the experiment.

Table S2. Capuchins participating in the experiment. *Individuals that were removed from the group in March 2008

Name	Sex	Month/Year of birth	Age category 2007/2008	Rank 2007/2008	Rank category 2007/2008
Accroc*	Male	08/1996	Adult	1/NA	High/NA
Alila	Female	08/1999	Adult	15/3	Mid/High
Arnaud	Male	07/1998	Adult	2/1	High/High
Asson*	Female	05/1989	Adult	6/NA	High/NA
Boy	Female	01/1973	Adult	17/8	Low/Mid
Kinika	Female	06/1992	Adult	7/13	High/Low
Kiwi	Female	~1980	Adult	3/10	High/Mid
Kolette	Female	08/1999	Adult	11/9	Mid/Mid
Olive*	Female	09/2000	Adult	16/NA	Low/NA
Paola	Female	06/2001	Adult	18/11	Low/Mid
Petula	Female	04/2001	Adult	13/12	Mid/Low
Pistou	Male	04/2001	Adult	4/4	High/High
Popeye	Male	05/2001	Adult	10/5	Mid/High
Raven	Male	08/2002	Adult	8/2	Mid/High
Rosy	Female	05/2002	Adult	5/7	High/Mid
Samir	Male	05/2003	Adult	9/6	Mid/Mid
Shaka*	Female	07/2003	Adult	14/NA	Mid/NA
Velvet	Male	10/2006	Juvenile/ Subadult	21/14	Low/Low
Vicky	Female	03/2006	Juvenile/ Subadult	20/16	Low/Low
Vlad*	Male	05/2006	Juvenile/ Subadult	12/NA	Mid/NA
Wallis	Male	05/2007	Infant/ Juvenile	19/15	Low/Low
Willow	Female	08/2007	Infant/ Juvenile	22/17	Low/Low

The capuchin group was a multi-male, multi-female group with ages ranging from 0.5 years to over 30 years (Table S2). Testing was carried out in two sessions, in November - December 2007 and June 2008. During the intervening six months, five members of the group were removed to start a new colony at a separate facility. For the 2007 cohort *N*= 22, and for the 2008 cohort *N*=17.

(iii) Children. Participants were tested at three nursery schools, namely St. Andrews Nursery School, Lawhead Primary School and Westfield Nursery School, in east Fife, UK. They were tested in an area of their schools that was separate from the main class, but was familiar to them. Where required by the school, a teacher was present in the room also, although they were requested not to speak or interact with the children during the trial sessions.

Eight groups of children were tested with group sizes of 4 and 5. The age range of the groups was 40 to 59 months. There was always a mix of sexes within the groups, although exact sex ratio varied (Table S3). The parents of all children involved in the study had signed consent forms agreeing that their child could participate.

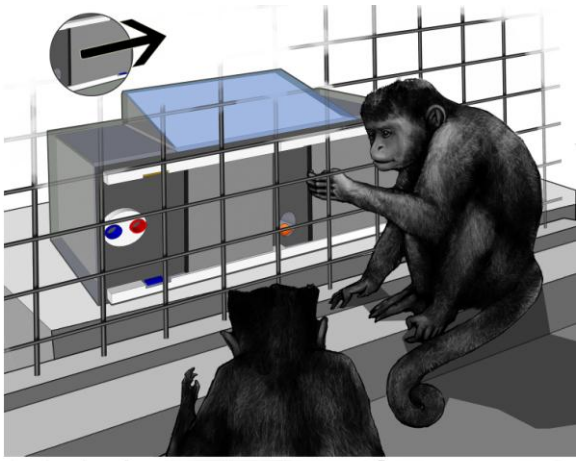
Table S3. Child groups participating in the experiment.

Group identity	Condition	Number of males	Number of females	Mean age of groups (yrs/months) (± standard error [months])
1	Scaffolded	3	1	3.6 (± 1.5)
2	Scaffolded	3	1	4.1 (± 1.9)
3	Scaffolded	4	1	4.7 (± 1.3)
4	Scaffolded	2	2	3.9 (± 3.1)
5	Open	4	1	3.9 (± 2.0)
6	Open	1	3	4.2 (± 2.0)
7	Open	3	2	4.3 (± 2.1)
8	Open	2	2	3.8 (± 1.9)

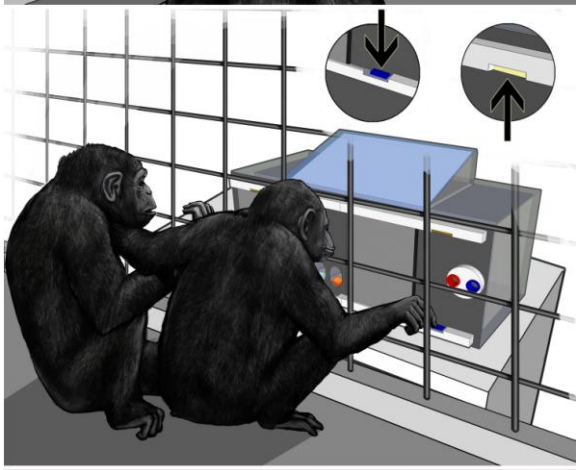
Ethics Approval

All research was approved by the ethics committee of the University of St. Andrews, in addition chimpanzee and capuchin work was approved by the ethics committees of MD Anderson Cancer Center and the Centre de Primatologie respectively. All research complied with both the legislation of the UK and the countries in which the research was conducted.

a.



b.



c.

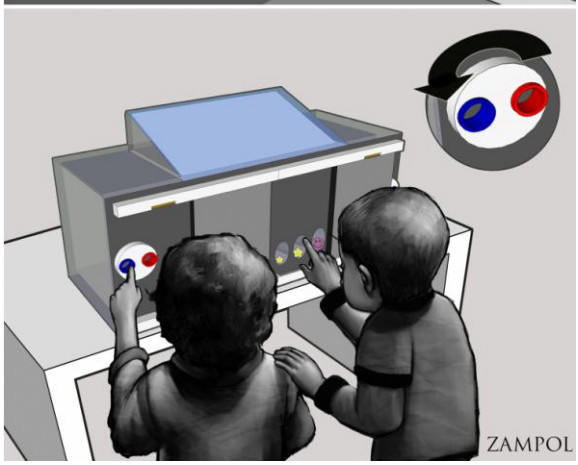


Figure S1: The puzzlebox used in the experiments, showing the three different species interacting with the puzzlebox. A- capuchins opening stage 1, B- chimpanzees pushing the down button to solve stage 2, C- children using the blue fingerhole to solve stage 3.

Apparatus

The puzzlebox used in this experiment could be solved sequentially, at three separate levels, or 'stages'. The three stages offer successively more desirable rewards, but require more complex manipulations to solve, with each stage building upon the previous one (see Fig. S1). The box was designed symmetrically, allowing two parallel options (alternative doors could be slid left or right at stage 1, alternative buttons at the top or bottom could be depressed at stage 2, and alternative coloured finger-holes enabled the dial to rotate clockwise or counter-clockwise at stage 3) with which to complete each stage. This two-action, two-option design allowed us to distinguish between alternative social learning mechanisms.

The first stage could be opened by sliding one of the two doors outwards in a horizontal plane, the left-side door moving to the left and the right-side door to the right. This action revealed a feeding chute through which a low-level reward could be delivered, with each door revealing a separate symmetrically placed tube. The second stage could be opened by pushing one of two buttons; either the button in the top runner, upwards, or the button in the bottom runner, downwards. Depression of either of these buttons allowed the door to be slid open wider to reveal a second food tube on that side, from which a mid-level reward was delivered. Once again, there were symmetrically placed upper and lower buttons on each side of the box, and symmetrically placed mid-level

feeding tubes on right and left sides. The final stage was opened by turning a dial, using either a red or blue bordered finger hole, which allows the door to be slid open even further, to reveal a third feeding tube on that side from which a high-level reward could be retrieved. Again, there were symmetrically placed dials on each side of the box, and symmetrically placed feeding tubes delivering high-level food on the right and left side. Olfactory holes were drilled into each puzzlebox door, to help ensure that the subjects were aware of the presence of the rewards behind them.

The puzzleboxes given to children, chimpanzees and capuchin monkeys differed only in size, being scaled appropriately to the mean size of the subject.

(i) Chimpanzees. The puzzlebox used with chimpanzees was 700mm (l) x 300 mm (h) x 300(w)mm, with the main frame constructed of Perspex. The doors were 220 (h) x 160 (w)mm and were made of acrylic veneered with steel for added strength. The acrylic buttons at stage two were positioned 130mm from each end of the puzzlebox and measure 40 (l) x 10 (w) mm. The dials (diameter 100mm) were positioned 50mm from each end of the puzzlebox and were also made from acrylic. The entire puzzlebox was bolted to a cart to ensure the safety of animals and experimenters and to assist in transport.

Chimpanzees were tested at an observation 'window' in the outdoor corrals. This was 1(h) x 1.93 (w)m and covered with bars 51mm apart. Subjects were able to reach through the bars and operate the puzzlebox, which was located outside the enclosure. When first presented to them, the puzzlebox was novel to all animals

in the group, although the required actions were similar to those displayed by the chimpanzees when presented with other puzzleboxes (e.g. Whiten et al., 2007). The actions required to solve the puzzlebox were, therefore, likely to be in the repertoire, or similar to actions in the repertoire, of the chimpanzees. In Experiment 2, individual demonstrator training took place in the indoor enclosures of the chimpanzee facility as described below.

(ii) Children and capuchins. The puzzlebox used with capuchins and children was constructed in the same way as the chimpanzee puzzlebox, except that the doors did not require a veneer of steel. This puzzlebox measured 540 (l) x 180 (h) x 190(w) mm. The doors measured 120(w) x 115(h) mm each and, when closed, were 140mm from the end of the puzzlebox. The buttons measured 30(l) x 5(w)mm and were positioned 75mm from each end of the puzzlebox. The dials were 50mm in diameter and were positioned 90mm from the bottom of the puzzlebox and 45mm from each end.

For the capuchins, the puzzlebox was placed outside of the outdoor enclosure with capuchins being able to reach through the $50mm^2$ mesh to reach and manipulate it.

For the children, the puzzlebox was positioned on a table and children were instructed before the start of the first trial where in the room they were allowed to walk. If necessary a barrier of chairs prevented the children walking directly behind the puzzlebox, in order to ensure they did not gain visual access to the mechanisms under the control of the experimenter.

When in use, the experimenter sat behind the puzzlebox to reset and re-bait the box with the rewards. The experiments were filmed with a Sony Handicam DCR-HC27E, which was positioned behind the experimenter for the chimpanzee and capuchin trial and to one side of the box in the children trials.

Procedure

Reward preference testing

Prior to the experiment, food preference testing was carried out with the chimpanzees and capuchins in order to establish suitable low-, mid- and high-level rewards. In the case of the chimpanzees, initial trials utilised food identified in previous food preference trials carried out by Brosnan et al. (Brosnan SF, Talbot C, Ahlgren M, Lambeth SP & Schapiro SJ 2010 Animal Behaviour 79, 1229-1237; Brosnan, pers. comm.). Each chimpanzee group was tested with a separate food preference test. Testing occurred when chimpanzee groups were allowed back into their indoor enclosures following husbandry procedures. Half a kilo of three foods, *(i)* grapes, and grape-sized pieces of *(ii)* carrots, and *(iii)* apples - were each separately placed in four piles, totalling 12 piles of food spaced evenly, in a randomised order, across the floor of the enclosure. The food first consumed by each subject in the group was recorded, as well as the order in which the four piles of food were completely consumed. This was repeated three times with every experimental group prior to the commencement of the experimental trials.

The capuchin food preference testing exploited the fact that the capuchins were previously trained to exchange items and have been involved in experiments in which they choose between two options offered to them by an experimenter. Whilst the group were freely associating in their outdoor enclosure, individuals were presented with two foods (from carrot, apple and grape) and were allowed to choose one food, which they were able to consume. The order of food presentation and the hands in which foods were presented was randomised over time. Due to dominance in the group, some individuals received more tests than others as they displaced the focal individual, however, eighteen (81%) of the population each received at least five food preference tests.

In both chimpanzees and capuchins we observed an unambiguous pattern of preference, with grape being deemed most desirable, then apple, then carrot.

Children were given stickers as rewards, as is common in developmental psychology studies (e.g. Herrmann et al., 2007). Prior to the experimental sessions the children were told that during the game they might get stickers, although they were not told that these rewards would come from the puzzlebox. A pilot study with five children, none of whom took part in the main experiment, was conducted; in this study children were asked to stick a range of stickers on a piece of paper in order of desirability. Stickers were chosen for the main experiment that appeared in the hierarchies in the same order in the pilot, regardless of the exact rank each child gave the sticker. Experimental groups were told the order of desirability of stickers with small stars being bettered by

large stars, which were, in turn, bettered by stickers displaying a smiling face and a glittery background.

Experiment 1

(i) Chimpanzees

All trials were one hour in duration and were conducted in the morning between 9am and 12pm. Trials were conducted at least 30 minutes after the usual morning feed of vegetables and fruit and before the provision of the chow feed. The exact timing of the trials was randomised to control for feeding motivation of animals throughout the morning. In four instances early termination of testing was required, due to malfunctioning of the puzzlebox or a security breach. All groups were exposed to the puzzlebox for a total of 30 hours.

The trials were conducted from August to October 2007, and from August 2008 to January 2009. One trial, per group, was conducted per day as frequently as practicable.

The procedure differed across two conditions, designed to examine the importance of satisficing and conservatism (hypothesis 8, Table S5), by controlling the protocol in which rewards are given.

"Open" Condition

Two groups (N=8 & N=10) were presented with the puzzlebox with food provided at all stages. Individuals were able to manipulate the puzzlebox to any stage and receive the food reward at that level. If an individual successfully

opened the puzzlebox to stage three then all manipulandi were immediately reset and the food tubes restocked. However, if animals performed unsuccessful manipulations or successfully manipulated the box and opened stage one or two then two minutes after the initial manipulation all manipulandi were reset and the food tubes restocked.

"Scaffolded" Condition

Two groups (*N*=8 & *N*=7) were presented with regulated access to parts of the puzzlebox. Here, the dial and buttons of the task were shielded, using guards, such that the subjects could only gain access to the stage one doors. When 75% of the group had successfully manipulated the doors of the puzzlebox at least five times in a trial (a criteria judged as indicating 'learning' of the technique), the guards covering the button manipulandi for stage 2 were removed. At this point the reward was removed from stage 1, thus animals must successfully manipulate stage 2 (having manipulated stage one with no reward) to receive a reward. This procedure was to be repeated in transition of individuals from stage two to stage three of the puzzlebox. As with the open condition, the manipulandi were returned to their original positions two minutes after they were first manipulated unless individuals solved the puzzlebox to the maximum level possible at the time and had received a food reward, in which case the puzzlebox was immediately reset.

(ii) Capuchins

Two, one hour, trials were conducted daily with a total of 53 trials over two time periods (November to December 2007 and June 2008). The first trial was

conducted in late morning (starting 10.30-11am) and the second trial in the afternoon (starting 1.30-2.30pm) with no less than 90 minutes between trials. The capuchin group was tested using the scaffolded condition only.

(iii) Children

Each group received five trials of 30 minutes each, with one trial per day, with a space of one to three days between trials. In accordance with the testing context for the non-human primates, the children were allowed to leave the room and return to their classroom at any time. The stickers that individuals collected were placed in an opaque cup that they were allowed to carry with them. This allowed the stickers to be stored in one discrete place, but also allowed limited visual access by other members of the group, making it less likely they could assess the skill of another individual from results alone, in the same manner as non-humans would eat the food rewards they received. Four groups were tested in the open condition and four in the scaffolded condition, with conditions balanced across the three nurseries.

Experiment 2

Four groups of chimpanzees took part in the second experiment. From each of these groups a female was isolated and trained to use the puzzlebox to access stage three reliably, rapidly and consistently. In two groups (N=13 and 8) a high-ranking female demonstrator was trained whilst in two groups (N=11 and 9) a low-ranking female demonstrator was trained. Females were chosen as demonstrators as they can be isolated more easily and reintroduced to the group with less aggression, and they tend to concentrate for longer during training

sessions (Whiten A, Horner V & DeWaal F, 2005. Conformity to cultural norms of tool use in chimpanzees. Nature 437, 737-740). Demonstrators of different rank were used to assess whether there was a difference in the spread of a cumulative innovation depending upon the rank of the 'innovator'.

During demonstrator training, tutee demonstrators observed demonstrations by the experimenter and the trainer at the facility. Rewards were handed to the chimpanzee once the trainer had demonstrated how to get to the stage. In addition further rewards, where necessary, including fruit, yoghurt and peanut butter, were placed on the button and dial of the puzzlebox to scaffold learning. Training sessions never took more than 20 minutes and the animals were then reintroduced carefully back into their groups to avoid any violence towards them. Animals were judged to have learned to use the puzzlebox when they could reach stage three on six successive attempts, for three trials all of which were conducted on different days.

The trials in the second experiment were three hours in duration, each group receiving eight trials, which were randomised between morning (8.30-11.30am) and afternoon (2-5pm) sessions. One trial was conducted per day over two weeks with a space between trials of one to three days. During trials a maximum of one small feed of vegetables and fruit was given by the care staff. This was insufficient to satiate the subjects or distract them for more than approximately five minutes.

In two groups, one with a low-ranking demonstrator and one with a high-ranking demonstrator, rewards were available at all levels for the first four trials and in the subsequent four trials there was food only available at the final stage. In the other two groups rewards were only available at the final stage for the first four trials and were available at all stages for the next four. This reward regime replicated the manipulation of 'open' and 'scaffolded' conditions in Experiment 1, but within rather than between subjects.

Demonstrator performance

All trained chimpanzee demonstrators solved the task consistently during the open diffusion trials, giving a mean of 150.9 (standard error ± 20.4) demonstrations reaching stage three per trial.

Data Collection

All data were coded from the video taken during the experimental trials. A second observer coded 2% of the data coded in each species. Inter-observer reliabilities were >94% for all recorded behaviour. All occurrences sampling was used to record each time an individual contacted the puzzlebox, and each unsuccessful and successful manipulation of the functionally relevant parts (stage 1-3) of the puzzlebox. Unsuccessful and successful manipulations were defined as those in which an individual did not and did retrieve a food reward, respectively. In each case the identity of the individual interacting with the puzzlebox was recorded as was the identity of the individuals in proximity to the puzzlebox (defined as an area of 1.5m around the puzzlebox) when the events occurred. In addition, the latency at which all individuals arrived and left the

area defined as proximity was recorded. Any aggression (defined as any interaction in which one individual struck another, displayed or exhibited an aggression face) or scrounging (defined as one individual removing food from the hand of another individual or from the puzzlebox before the individual who opened the door retrieved it) that took place within the area in proximity was recorded.

Table S4: The definitions of codes and additional clarifications that were coded from the video. Inter-observer reliability was calculated from both the code and additional comments combined.

Code	**Additional comments noted**	**Definition**
Contact	The area of the puzzlebox (e.g. 'left door' or 'top').	An individual touches the puzzlebox, but does not operate any of the moving parts of the puzzlebox.
Unsuccessful manipulation	Right/ left door	An individual opens the right/left door in the two minutes before the food reward has been replaced and therefore receives no food reward.
	Down on right/left The method of pushing the button (i.e. pushing with hands or biting)	An individual pushes on the down button on the right/left after another individual has pressed it, but before it has been reset.
	Up on right/left The method of pushing the button (i.e. pushing with hands or biting)	An individual pushes on the up button on the right/left after another individual has pressed it, but before it has been reset.
	Dial on right/left The method of turning the dial (i.e. red or blue hole)	An individual turns the dial after another individual.
Successful manipulation	Right/ left door. Stage to which door is pushed. Note whether the individual takes the food or not	An individual pushes the door open to reveal a reward.
	Up on right/left. The method of pushing the button (i.e. pushing with hands or biting)	An individual either pushes the up button or bites the button, unlocking the second stage of the puzzlebox.
	Down on right/left. The method of pushing the button (i.e. pushing with hands or biting)	An individual either pushes the down button or bites the button, unlocking the second stage of the puzzlebox.
	Dial on right/left. The method of turning the dial (i.e. red or blue hole)	An individual turns the dial to unlock the third stage of the puzzlebox.
Altruism	Identity of individual that donates reward and individual that receives it.	An individual gives a reward it has obtained from the puzzlebox to another individual.
Aggression	Identity of individual	Any interaction in which one individual strikes

	perpetrating aggression and those being attacked.	another, displays or exhibits an aggression face.
Scrounging	Identity of the scrounger and the victim	An individual removes food from the hand of another individual or from the puzzlebox before the individual who opened the door retrieves it.
Teaching	Method of teaching (i.e. verbal, gestural or a mixture)	An individual produces a gesture or vocalisation (or both) that functions to facilitate learning in another individual by imparting knowledge about the solutions to the puzzlebox.
Vocalisation		*Non-human primates:* an individual produces a food call (as defined in capuchins by Fragaszy et al., 2004 and chimpanzees by Slocombe & Zuberbühler, 2005).
	Children: The words spoken by the individual or a description of the vocalisation if non-verbal.	*Children:* an individual produces a vocalisation, either a verbal or non-verbal.

344

345 *Analyses*

346 All analyses were carried out using the *R* statistics package (R-Development-
347 Core-Team). The data were tested for normality using a Shapiro's test and non-
348 parametric tests were used only where the assumptions of parametric tests were
349 violated. Below we provide further detail, where necessary, detailing how the
350 eight hypotheses outlined, in the main text, were evaluated.

351

352 To allow greater resolution in the assessment of the performance of individuals,
353 rather than analysing data on a 0-3 scale based upon the puzzlebox stage the
354 individual achieved, a species-specific 'achievement rank' was calculated for each
355 individual. The 'achievement rank' ranks individuals first upon the stage that
356 they achieved and differentiates further between individuals by the number of
357 times they successfully manipulated the puzzlebox at that stage. In the case of a
358 tie at this point, the number of successful manipulations performed at previous
359 puzzlebox stages is used to differentiate between the individuals. This has the
360 advantage that it renders the distribution continuous, which is better suited to
361 analyses and affords greater statistical power.

Table S5: Eight alternative hypotheses specifying why humans, but not other animals possess cumulative culture and the extent to which each is supported by comparing the performance of capuchins, chimpanzees and children.

Hypotheses	Capuchins	Chimpanzees	Children	Hypothesis supported?
Social Cognition				
1. A lack of teaching in non-human primates hinders ratcheting (*2,6,13*)	No direct teaching events. Mother—juvenile-offspring dyads are significantly more likely to have reached a different stage than mother —adult-offspring dyads.	No direct teaching events. Individuals significantly more likely to scrounge from their juvenile offspring than from their mother. No significant difference between the stage reached by mother—juvenile-offspring dyads and mother—adult-offspring dyads	Substantive teaching, with a significant correlation between the number of teaching events received and achievement rank.	Supported
2. Communication in non-human primates is not sufficient to support ratcheting (*13*).	Few food calls emitted. No increase in recruitment following calls.	Few food calls emitted. No increase in recruitment following calls.	All instances of teaching involve vocalization. Significant correlation between amount of verbal instruction and achievement rank.	Supported
3. Lack of imitation in non-humans hinders ratcheting (*1,2,6*).	Do not match recently observed actions.	Do not match recently observed actions	Match recently observed actions. Significant correlation between proportion of matching manipulations and achievement rank.	Supported
4. Lack of prosociality in non-humans hinders ratcheting (*2,13*).	No voluntary donation of rewards.	No voluntary donation of rewards.	Frequent voluntary donation of rewards. Significant relationship between gifts received and achievement rank.	Supported
Social Structure				
5. Scrounging, or being scrounged from, hinders learning (*20*).	No correlation between scrounging and achievement rank. Positive correlation between number of times scrounged from and achievement rank.	Positive correlation between scrounging, and number of times scrounged from, and achievement rank.	Positive correlation between scrounging, and number of times scrounged from, and achievement rank.	Not supported
6. Dominants monopolise resources preventing low rankers from gaining access to the task (*17*).	Dominant individuals use the puzzlebox significantly more than low rankers in 2007, but not in 2008.	Low and mid rankers use the puzzlebox significantly more than high rankers.	No significant difference between the number of manipulations performed by low and high rankers	Not supported
7. Lack of attention to low rankers and/or juveniles hinders diffusion (*18,19*).	No significant difference between the amount of attention paid to individuals of different rank or age.	No significant difference between the amount of attention paid to individuals of different rank or age.	No significant difference between the amount of attention paid to individuals of different rank.	Not supported
Non-Social Cognition				
8. Non-human animals are conservative and satisfice (*8,16*).	Individuals perform a significant number of non-conservative manipulations.	Receiving rewards at all stages does not hinder performance relative to scaffolded condition. Individuals perform a significant number of non-conservative manipulations.	Receiving rewards at all stages does not hinder performance relative to scaffolded condition. Individuals perform a significant number of non-conservative manipulations.	Not supported

Additional methods for hypothesis testing

Hypothesis 1

A lack of teaching in non-human primates hinders the spread of cumulative innovations throughout the population

We defined teaching by direct instruction as 'any instance in which an individual engaged in an act that clearly functioned to facilitate learning in another individual', in this instance by imparting knowledge about the solutions to the puzzlebox task. In the capuchins and chimpanzees we went on to consider more subtle forms of 'teaching', such as *scaffolding*, defined as facilitating learning in others through acting in a manner that functions to draw attention to the task or rewards, or create learning opportunities for others. We specifically considered scaffolding afforded by tolerated theft by comparing the frequency of food transfer from mothers to juveniles to that from juveniles to mothers.

Hypothesis 2

Communication insufficient to support ratcheting

With regard to the analysis of the recruitment potential of food-calls, we computed the rate (arrivals/min) of animals entering proximity to the task in the two minutes following an individual in proximity emitting a food call, and compared this to the baseline rate of individuals entering proximity throughout the trial. In children, we compared the success of individuals who had received verbal instruction with those that had not.

Hypothesis 3

Lack of imitation or other complex forms of social learning in non-humans hinders the spread of cumulative innovations throughout the population

To test whether observational learning played any role in the acquisition of solutions to the puzzlebox, we examined whether individuals manipulated the box in a matching manner, either because they copied the actions of others at the puzzlebox (i.e. imitation) or because they made the same parts of the box move in the same way (object-movement re-enactment, emulation). As physical access to the puzzlebox was often blocked when other individuals were interacting with it, the analysis determined whether an individual matched the manipulations of another individual who had been manipulating the puzzlebox immediately prior to their manipulation. As there was little progression beyond stage 1 in experiment 1 with the chimpanzees, this analysis was carried out using data from the second experiment, utilising those occasions when a skilled demonstrator left the proximity of the task and another individual manipulated the puzzlebox, provided both the demonstrator and observer had been in proximity to the puzzlebox for at least a minute. For the capuchins, analysis focussed on occasions where individuals skilled at stage two left the puzzlebox, after having been observed by another individual in proximity for at least one minute, and who went on to contact the puzzlebox in the subsequent minute. As children left the puzzlebox less frequently than other species, all instances of skilled children leaving the puzzlebox were considered until a time at which all individuals in the group had learned to open stage three. Once again, we focused on occasions where the first child had been observed by another child in proximity for at least one minute, and where the second child went on to contact the puzzlebox in the subsequent minute. In all cases, all classes of manipulations

by the 'demonstrator' (e.g. slide left door to left, push left upper button etc) were recorded in the minute preceding it leaving the puzzlebox, and all manipulations by the observer in the subsequent minute were recorded. Those manipulations that matched those performed by the demonstrator were classified as 'matching', while those that had not been performed by the demonstrator were classified as 'non-matching' (Table S6).

Table S6: Actions performed by a demonstrator and the actions that were classed as matching if performed by an observer after observing that demonstrators action. All other actions were classified as non-matching.

Demonstrator's action	**Matching actions**
Contact puzzlebox (+ location on box touched)	Contact puzzlebox (+ same location on puzzlebox)
Unsuccessful/Successful right door	Contact right door: *touches but does not move door*
	Unsuccessful right door: *opens right door before it has been reset*
	Successful right door: *opens right door*
Unsuccessful/Successful left door	Contact left door: *touches left door but does not move door*
	Unsuccessful left door: *opens left door before it has been reset*
	Successful left door: *opens left door*
Unsuccessful/Successful down button on right (+method of pushing the button- i.e. pushing button with hands or biting)	Contact down on right (+ same method of pushing the button): *touches but does not move down button on right, using the same method*
	Unsuccessful down on right (+ same method of pushing the button): *pushes down on right, but before it has been reset, using same method*
	Successful down on right (+ same method of pushing the button): *pushes down on right, using the same method*
Unsuccessful/Successful down button on left (+method of pushing the button- i.e. pushing button with hands or biting)	Contact down on left (+ same method of pushing the button): *touches but does not move down button on left, using the same method*
	Unsuccessful down on left (+ same method of pushing the button): *pushes down on left, but before it has been reset, using same method*
	Successful down on left (+ same method of pushing the button): *pushes down on left, using the same method*
Unsuccessful/Successful up button on right (+method of pushing the button- i.e. pushing button with hands or biting)	Contact up on right (+ same method of pushing the button): *touches but does not move up button on right, using the same method*
	Unsuccessful up on right (+ same method of pushing the button): *pushes up on right, but before it has been reset, using same method*

	Successful up on right (+ same method of pushing the button): *pushes up on right, using the same method*
Unsuccessful/Successful up button on left (+method of pushing the button- i.e. pushing button with hands or biting)	Contact up on left (+ same method of pushing the button): *touches but does not move up button on left, using the same method*
	Unsuccessful up on left (+ same method of pushing the button): *pushes up on left, but before it has been reset, using same method*
	Successful up on left (+ same method of pushing the button): *pushes up on left, using the same method*
Unsuccessful/Successful dial on right (+method of turning the dial- i.e. red or blue hole)	Contact dial on right (+same method of turning the dial): *touches but does not move the dial on right*
	Unsuccessful dial on right (+same method of turning the dial): *turns dial on right after another individual, using the same method*
	Successful dial on right (+same method of turning the dial): *turns dial on right after another individual, using the same method*
Unsuccessful/Successful dial on left (+method of turning the dial- i.e. red or blue hole)	Contact dial on left (+same method of turning the dial): *touches but does not move the dial on left*
	Unsuccessful dial on left (+same method of turning the dial): *turns dial on left after another individual, using the same method*
	Successful dial on left (+same method of turning the dial): *turns dial on left after another individual, using the same method*

To measure whether social learning was occurring at the first stage, we used option-bias analysis (Kendal, R.L., Kendal, J.R., Hoppitt, W. & Laland, K.N. 2009. Identifying Social Learning in Animal Populations: A New 'Option-Bias' Method. *PLoSOne* 4(8): e6541) at the level of opening left door or opening right door, testing whether individuals in a group were more likely to use one option (opening one door), more than the other, which is likely to occur if social learning is occurring. This method is more powerful than conventional inferential statistics (Kendal et al., 2009).

Hypothesis 4

Lack of prosociality in non-humans hinders the spread of cumulative cultural traits

We recorded the number of altruistic events performed by each individual, defining an altruistic event as any instance in which an individual voluntarily gives a reward of any stage, accessed by themselves, to another individual.

Hypothesis 6 and 7

Dominant individuals monopolise resources hindering lower ranking individuals from gaining access, thereby limiting the number of individuals with the chance to solve the task. Lack of attention to low-ranking and/or juvenile individuals hinders learning from potentially skilled sections of the population

Individuals were divided into rank categories, high, medium and low for chimpanzees and capuchins and high and low for children. For chimpanzees ranks were based upon data that had been previously gathered on aggression during reintroductions and on feeding priority. Capuchin data were gathered on displacement rates at a single monopolisable food source. Child data were gathered by asking teachers to rank pupils on a scale of most socially dominant-least socially dominant and bold-shy.

Hypothesis 8

Non-human animals are conservative and satisfice, such that once they have a solution that rewards them they do not change it

We compared the performance of individuals in the open and scaffolded conditions in experiment 1, in both the children and chimpanzees. (As we only had access to one capuchin group, we were unable to make this comparison in the capuchins). We reasoned that, if individuals do satisfice then individuals in

464 the scaffolded condition should manipulate the puzzlebox more at higher stages
465 than individuals in the open condition, since the latter would still be receiving
466 rewards at the lowest stage, and be inhibited from further learning. Expectations
467 for the rate of manipulating each part of the apparatus were derived from
468 performance in early trials. For the chimpanzees, the manipulations in the first
469 three trials after the scaffolded groups had stopped receiving a reward at a lower
470 stage were compared to the same time period in the open condition. For the
471 children, the first 10 minutes of the trial in which individuals in the scaffolded
472 groups did not receive rewards, at the lower stages, any more were compared to
473 the same time period in the open condition.
474
475 **Additional Results**
476 *General performance*
477 In experiment 1, following 30 hours of presentation of the cumulative puzzlebox,
478 in 1-hr sessions, to each of the four groups of chimpanzees, only a single
479 individual in a single group reached stage 3. In the same group and one other
480 group, a single individual reached stage 2, in a third group two individuals
481 reached stage 2, whilst the remaining group witnessed multiple solvers at stage
482 1, but not at higher levels. Likewise, in groups with trained demonstrators
483 (experiment 2), although multiple individuals solved stage 1, the solutions to
484 stages 2&3 did not spread. Thus the experiments provide no evidence for
485 cumulative cultural learning in any chimpanzee group, including in experiment 2,
486 where trained demonstrators performed stages 1-3 proficiently. The
487 chimpanzees were clearly capable of solving the apparatus at higher stages
488 (stage 2-3), as witnessed by the performance of innovative individuals in three

groups, as well as the trained demonstrators, but in no group is there any evidence that these solutions spread to a second individual. A virtually identical pattern is observed in the capuchins, where after 53 hours (year 1: 28, year 2: 25), no individual reached stage 3, whilst only two individuals reached stage 2, and the majority of individuals solved only stage 1. These findings stand in stark contrast to those of the children, where despite a far shorter exposure to the apparatus (2.5 hours), five of the eight groups had at least two individuals (out of maximum 5) who reached stage 3, with multiple solvers at stage 2 in all these groups, providing clear and strong evidence for a cumulative cultural capability. Of the groups not reaching stages 2 & 3, two expressed little interest in the box, whilst in the third the children initially exhibited interest, leading to widespread stage 1 solutions, before interest waned (see below for discussion).

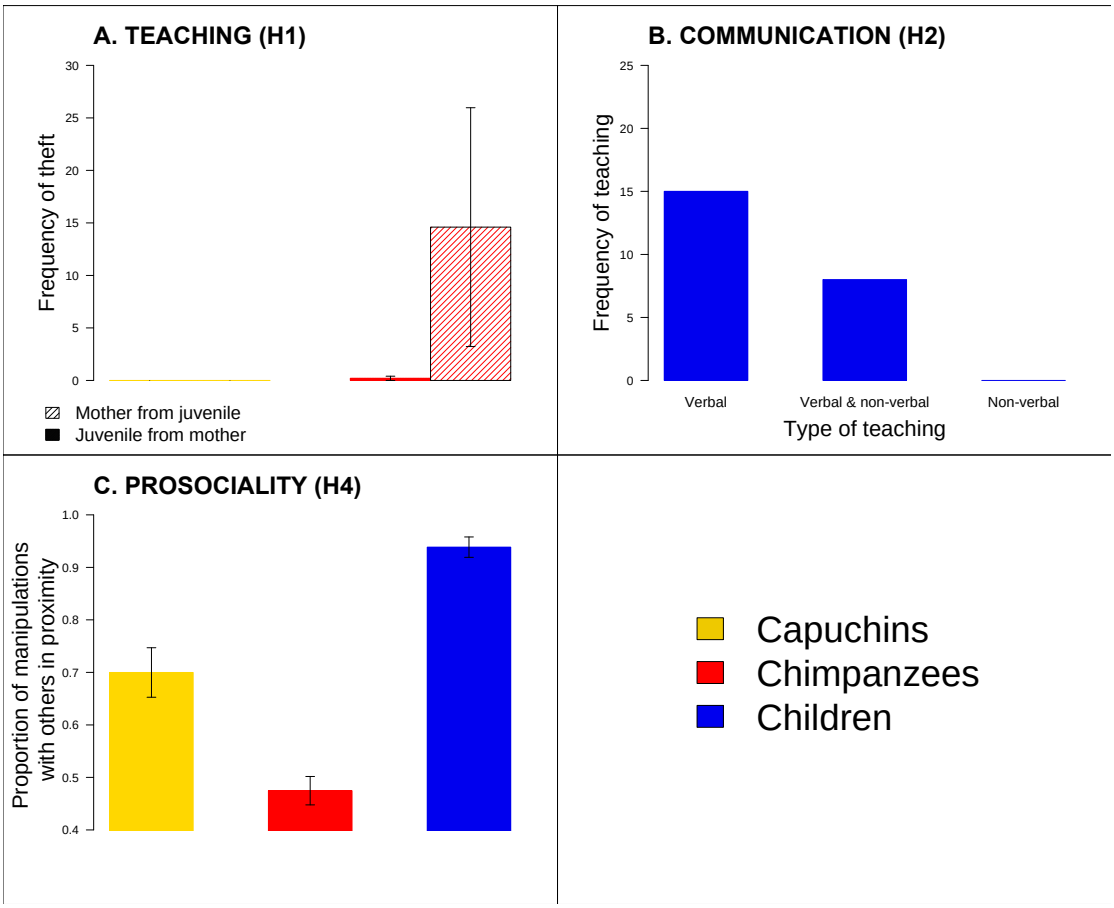
Hypothesis 1

Figure S2A shows that we observed substantially greater rates of tolerated theft of extracted food by mothers from offspring than vice-versa in chimpanzees (*Wilcoxon W*=16, *P*=0.026) and no tolerated theft in mother-infant pairs of capuchins.

Hypothesis 2

All teaching events by children involved verbal instruction and approximately one third involved gesture (Figure S2B).

Figure S2. Additional analyses.



Hypothesis 3

Using the option-bias method, there was no evidence of social learning of door choice (left vs right) in capuchins (*Option bias* χ^2= 546.5, *P*=1). However, there was evidence of social learning by chimpanzees in experiment one at the level of door choice, that is, stage 1 (*Option bias* χ^2= 941.6, *P*= 0.021). Combined with the lack of evidence for cumulative cultural learning in chimpanzees, and the low levels of matching at higher stages, these findings support the view that chimpanzees are capable of social transmission but not cumulative culture.

Hypothesis 4

A greater proportion of the manipulations by children were at the same time as another individual than either chimpanzees or capuchins (*Kruskal-Wallis* χ^2=39.56, *df*=2, *P*<.001; Figure S2C).

Hypothesis 5

There was no evidence that scrounging negatively affected the performance of either those individuals scrounging or those that were victims of scrounging. In capuchins there was no significant correlation between the number of times an individual scrounged from another and their achievement rank (*Spearman's Rank Correlation*: *rho*=0.34, *S*=1170.5, *P*=0.12). Achievement rank in chimpanzees was positively correlated with the number of scrounging events an individual perpetrated (*Spearman's Rank Correlation*: *rho*= 0.41, *S*=35466.2, *P*=0.0005). The achievement rank of children was significantly positively correlated with the number of times an individual scrounged from others (*Spearman's Rank Correlation*: *rho*= 0.84, *S*=1165.90, *P*<0.001).

Hypothesis 8:

We found no evidence that non-human animals are conservative and satisfice, such that once they have a solution that rewards them they do not change it. There were two capuchins that got to stage 2, thus suggesting that not all individuals act conservatively (i.e. remained at level 1). Across the entire population the number of non-conservative manipulations (that is, manipulations different from the first solution) performed by individuals (mean= 39.94 standard error= 22.41) was significantly different to zero (*Mann-Whitney test: U*=78, *P*=0.002). Likewise, analysing whether chimpanzees act

conservatively after they have learned to get to the first stage reveals that individuals do not always act conservatively. Across the populations the number of non-conservative manipulations performed by individuals (mean= 76.71 non-conservative actions, standard error= 42.37) was significantly different to zero (*Mann-Whitney test: U*=253, *P*<0.001).

Children did performed a significantly larger proportion of non-conservative actions (mean=0.34) than chimpanzees (mean=0.06) or capuchins (mean=0.18) (*Kruskal-Wallis:* χ^2=6.60, *df*=2, *P*=0.037). Whilst this might be interpreted as a difference in the conservative tendencies of the three species, other interpretations are possible. For instance, the elevated number of non-conservative actions performed by the children likely represents their elevated performance in general, which requires a degree of non-conservative behaviour, and hence may be attributable to the socio-cognitive processes discussed in the main text.

Results indicating that capuchins and chimpanzees recognised that the higher quality resources were superior to the lower quality resources.

In the pre-experiment food preference trial, capuchins showed a clear preference for grapes over apples and over carrots. During the trials a higher proportion of stage one rewards (carrot) were able to be scrounged than stage two (apple) rewards (*Wilcoxon W*=103, *P*=0.003).

Pre-trial testing revealed that chimpanzees preferred grapes to apples and apples to carrots. This supplemented other sources which also concluded this

581 order of food preference (Brosnan, pers. comm.). During the trials there was no
582 significant difference between the proportion of food that individuals allowed to
583 be scrounged at each stage (*Kruskal Wallis:* χ^2=1.05, *df*=2, *P*=0.59). There were
584 29 instances of 'termiting' behaviour in which individuals probed the olfactory
585 holes in the puzzlebox doors with small sticks or grass. There was at least one
586 instance of this behaviour in seven of the eight groups (mean=3.63 instances per
587 group, standard error= 1.16), with all instances occurring at the highest stage
588 that was stocked with food.
589
590 Pre-trial testing revealed that children consistently preferred smiley face
591 stickers to large stars to small stars. During the trials the proportions of rewards
592 found that were stolen at stage one (mean=0.20, standard error=0.031) and
593 stage two (mean=0.17, standard error=0.027) were significantly greater to the
594 proportion of the rewards found that were stolen at stage three (mean=0.09,
595 standard error=0.03) (*Kruskal-Wallis:* χ^2= 6.88, *df*= 2, *P*=0.032).
596
597 **Failure of 2 groups of children to interact with the cumulative task**
598 There was a notable finding with the children that in one group of children no
599 participants solved the puzzlebox and another group, in the scaffolded condition,
600 did not qualify as having solved the first stage to progress to the second stage.
601 These results contrast markedly with other species in which all but one of the
602 chimpanzees and 15 out of 22 capuchins learned to solve stage one. Shyness in
603 children of an unfamiliar experimenter and neophobia of the puzzlebox may
604 partially account for the lack of manipulations in some individuals, but are
605 unlikely to account for a group-level effect. In contrast to the chimpanzees and

606 capuchins studied, who live in colonies that regularly take part in a range of
607 extractive foraging experiments the children had not taken part in similar
608 experiments. Whilst shyness or neophobia are individual traits, a group
609 conformity effect may operate, whereby if one child does not step forward and
610 operate the puzzlebox, others will also refrain from doing so, and/or anxiety may
611 spread socially. This lack of solving in these two groups of children may,
612 therefore, also be due to the same socio-cognitive processes responsible for the
613 increased ability to solve the puzzlebox, with children operating as a group and
614 observing the performance of other individuals around them.
615
616 This conclusion is supported by the observation that, in one of the groups,
617 children engaged in a game, which was invented after one child dropped the cup
618 he had been given to store stickers during the first trial. This became known as
619 the 'cup game' among the group and consisted of throwing the cup, following it
620 and recovering it. Following its invention the game spread to all group members,
621 distracting them from the puzzlebox and providing a new social activity during
622 the trials.